



Phenological transition dictates the seasonal dynamics of ecosystem carbon exchange in a desert steppe

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Keywords

Ecosystem respiration; Ecosystem water-use efficiency; Gross ecosystem carbon exchange; Net ecosystem carbon exchange; Plant phenology; Precipitation; Spring annuals; Temperate desert

Nomenclature

Flora of China: <http://foc.eflora.cn>

Received 6 March 2014

Accepted 28 August 2014

Co-ordinating Editor: Beverly Collins

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Abstract

Question: There are large variations in ecosystem carbon (C) exchange in desert ecosystems; however, few studies have examined the effects of community phenological staging on seasonal variations of ecosystem C exchange. We asked whether factors that control temporal changes in net ecosystem C exchange (NEE) vary with an obvious community transition from spring annuals to summer annuals and perennials in a temperate desert steppe.

Location: South margin of the Gurbantunggute Desert, northwestern China.

Methods: Ecosystem C and water exchange were measured regularly using closed static chambers and analysed at daily and seasonal intervals. Soil moisture and temperature, photosynthetically active radiation (PAR) and plant biomass were also investigated.

Results: Soil temperature had a dominant influence on C release into the atmosphere from the ecosystem during the snowmelt phase (mid-March to early April). In the spring annual dominant phase (mid-April to early June), the diurnal pattern of NEE was consistent with the pattern of PAR. The ecosystem became a weak C resource ($0.16 \pm 0.03 \mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$) and NEE was positively correlated with community biomass during this phase. In the summer annual and perennial dominant phase (late June to late September), NEE showed relatively large C release ($0.74 \pm 0.03 \mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$) and was negatively correlated with soil temperature.

Conclusion: Our results indicate that the primary abiotic factor controlling NEE varies throughout the year, and NEE is determined by the interaction of a plant functional group with precipitation and temperature.

Introduction

Arid and semi-arid regions cover ca. 30% of the global terrestrial surface (Lal 2004). However, over the past few decades, these regions have been neglected with regard to ecosystem carbon (C) balance (Falge et al. 2002a,b; Liu et al. 2012). Recent climate models have predicted an increasing trend in precipitation in mid-latitude regions (IPCC 2007), with a corresponding increase in vegetation cover and productivity, resulting in a net C sink in arid and semi-arid regions (Niu et al. 2008; Wohlfahrt et al. 2008; Liu et al. 2012; Yang & Zhou 2013). However, other factors influencing climate change, such as warming, might increase drought duration, depress plant growth and accelerate decomposition of organic matter in the soil, causing an increase in C release in arid and semi-arid regions (Xia

et al. 2009). Some studies have examined net ecosystem C exchange and simultaneously measured plant growth and gross primary productivity in order to elucidate the potential mechanisms of ecosystem C uptake in desert ecosystems (Jasoni et al. 2005; Wohlfahrt et al. 2008; Gao et al. 2012). However, few have simultaneously determined gross ecosystem C exchange (GEE) and ecosystem respiration (ER), despite the fact that the balance of GEE and ER reflects net ecosystem C exchange (NEE). Therefore, it is important to investigate NEE and its two components in order to understand the general patterns of ecosystem C exchange in temperate deserts. According to some studies, a change in the dominant plant functional group in a community resulting from biological invasion or land-use change can exert profound effects on ecosystem C exchange (Scott et al. 2010; Hamerlynck et al. 2012; Yang

& Zhou 2013). For instance, plant invasion can enhance net ecosystem production by directly promoting plant growth (Hamerlynck et al. 2012). This is similar to plant functional shifts in deserts: the dominant functional group in the herbaceous community of desert ecosystems is reported to change within a growing season. Because of the differences in plant life history, phenology and biomass, such a shift may ultimately generate seasonal variation in NEE (Scott et al. 2010; Hamerlynck et al. 2012; Yang & Zhou 2013).

In the Gurbantunggute Desert of northwestern China, the herbaceous community is composed of summer annuals and perennials and spring annuals. Spring annuals in deserts respond to the availability of water (Qin et al. 2007; Wu et al. 2013). They generally begin vegetative growth immediately after snow melt and complete their reproduction before mid-June. As a result, they dominate the plant community in spring, with a vegetation cover as high as 40%. Early spring precipitation is critical for the growth and performance of spring annuals as it determines plant density and biomass (Fan et al. 2014). Summer annuals and perennials, especially drought-tolerant species, rely on some specific adaptations, such as leaf hairs, succulence and a reduction in leaf size, to grow fast and dominate the plant community (Fan et al. 2012, 2014; Zhang & Liu 2012). Given that photosynthetically active radiation (PAR) and soil moisture decrease after summer, temperature constrains the performance of summer annuals and frost may advance their death, the effects of plant growth on NEE may be complicated by an intra-seasonal shift in the dominant plant functional group within the community. Moreover, the controlling factors of NEE may change correspondingly.

In this study, we focused on C exchange in a desert steppe in the Gurbantunggute Desert of northwestern China. Considering the seasonal contrasts in plant cover and community biomass, there are three distinct phases in community composition in the Gurbantunggute Desert: snow melt, spring annual dominance, where the community is dominated by *Alyssum linifolium*, *Schismus arabicus*, *Lactuca undulata* and *Erodium oxyrrhynchus* from April to mid-June, and the dominance of summer annuals and perennials, where the community is dominated by *Salsola subcrassa*, *Ceratocarpus arenarius* and *Euphorbia turczaninowii* from mid-June to September. Given the effects of plant growth on gross ecosystem productivity (GEP), we suggest that changes in NEE are closely related to community structure and growth. Here, we tested the following hypotheses: (i) as NEE exhibits seasonal variations it may be controlled by different biotic and abiotic factors in the three phases; (ii) given that water is the primary limiting factor for plant growth in deserts, the effects of temperature on NEE likely depend on soil water availability; (iii)

the relationship between soil water and NEE might depend on water-use efficiency (WUE) of the plant community, since the stimulation of water is larger on GEE than on ER in this high water-use efficient community (Liu et al. 2012); and (iv) spring annuals are expected to have a critical impact on ecosystem C exchange as they comprise a significant proportion of the community biomass.

Methods

Study site

This study was conducted on the southern margin of the Gurbantunggute Desert (44°12'–44°21' N, 87°50'–87°54' E, 450 m a.s.l.). This desert is both fixed (plant cover >30%) and semi-fixed (plant cover of 10–30%). The topography is characterized by alternating sand dunes and wide, flat interspaces between the dunes. The longitudinally parallel sand dunes are generally 2–5 km in length, with a relative height ranging from 20 to 30 m. The interspaces between sand dunes are usually 200 to 500 m wide. The Gurbantunggute Desert has a typical temperate continental climate, with a dry hot summer and cold winter. The annual mean temperature is 6.6°C and annual mean precipitation is 163 mm, according to data collected at an auto-meteorological station for 2001–2012. Snow cover is stable and is normally present from late November to late March of the following year, at a depth of ca. 20–35 cm (equivalent to 38–64 mm rainfall). Snow accounts for 24–40% of the annual precipitation in this region.

A total of 20 species were recorded at the study site during the course of the experiments in 2012. Based on life history, the plants can be divided into two groups: spring annuals and summer annuals and perennials. The dominant spring annuals included *Alyssum linifolium*, *Schismus arabicus*, *Lactuca undulata* and *Erodium oxyrrhynchum*, accounting for more than 60% of community cover and 85% of biomass. Summer annuals and perennials included *Salsola subcrassa*, *Ceratocarpus arenarius*, *Orostachys spinosus*, *Euphorbia turczaninowii*, *Descurainia sophia*, *Hyalea pulchella*, *Astragalus arpilobus*, *Trigonella arcuata* and *Agriophyllum squarrosum*. These species usually occur together in communities and account for only a small portion of community biomass before June, but dominate the community after the spring annuals die back. Phenological observation revealed that spring annuals begin to grow immediately after snow melt in late March, mature in mid-May, and usually die before early June. Summer annuals usually grow slowly before mid-June, and dominate the community after the spring annuals die. Based on phenology (Price & Waser 1998), the dominant phase of a plant group (spring annual or summer annual and perennial) begins when germination frequency reaches 80%, and ends when plant death reaches 80%. Hence, the dominant

phase of the spring annuals at the study site started on 1 April and ended on 6 June 2012.

Experiment layout and ecosystem gas exchange measurement

Six plots of 10 m × 10 m each were selected for C exchange monitoring, and each plot was in a valley between sand dunes, with a 10-m interval between two adjacent plots. Two aluminium collars (ca. 3-cm deep and 50-cm edge length) with a rubber groove for chamber placement were installed randomly in each plot in late March 2012.

Ecosystem gas exchange was measured with the closed static chamber method. The chamber dimensions were 50 cm × 50 cm at the base and 30 cm in height (Steduto et al. 2002; Potts et al. 2006; Bubier et al. 2007; Harpole et al. 2007; Xia et al. 2009). Chamber walls were constructed of clear polyethylene sheet, which allows 90% of PAR to pass through. Two electric fans were installed to maintain steady temperatures ($\pm <0.5$ °C compared to ambient temperature) and humidity in the chamber during measurement. Gas exchange was measured using a Li-Cor 840 portable photosynthesis system (IRGA; LiCor Inc., Lincoln, NE, US) attached to the chamber. Two sampling runs at full PAR and under dark conditions were conducted at each collar location. Twelve consecutive recordings of CO₂ exchange under natural radiation were taken at 10-s intervals during a 120-s period when CO₂ was released or taken up (usually <40 s after the equipment was attached), which represents NEE. After NEE measurement, the chamber was vented, and then covered with an opaque cloth to eliminate plant CO₂ exchange (usually 15–20 min after darkening in our preparative test). The same procedure was conducted under dark conditions, when CO₂ release steadily increased. Given the absence of photosynthesis under such conditions, the value measured in the opaque chamber represents ecosystem respiration (ER), which includes both plant and soil respiration (Welker et al. 2004). The difference between NEE and ER represents GEP within the chamber, and ecosystem water-use efficiency (WUE) was calculated as the ratio of GEE to evapotranspiration (ET) (GEE/ET). Specifically, positive and negative NEE values represent net C uptake by and release from the ecosystem, respectively. NEE and ER were calculated using equation (1):

$$F_c = \frac{10VP_0(1 - W_0)}{RS(T_0 + 273.15)} \frac{\partial C}{\partial t} \quad (1)$$

where F_c is the C exchange rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$), V is the volume of the assimilation chamber (72 030 cm³), P_0 is the initial pressure (kPa), W_0 is the initial water vapour

mole fraction ($\mu\text{mol} \cdot \text{mol}^{-1}$), R is the universal gas constant (8.312 kJ mol⁻¹·K⁻¹), S is the inner surface area of the chamber base (2401 cm²), T_0 is the initial air temperature (°C), and $\partial C/\partial t$ is the slope of the least squares linear regression of CO₂ concentration on time ($r^2 > 0.98$).

Although this chamber method tends to underestimate C exchange because of vapour pressure effects (Hooper et al. 2002), the soil respiration value obtained using this static chamber method was similar to that measured by the Li-8100 (LiCor Inc., Lincoln, NE, US) at our site, suggesting the validity and reliability of the static chamber method. Moreover, all r^2 values for the relationship between CO₂ chamber concentration and time during measurements were >0.98.

Ecosystem gas exchange measurements were conducted from 17 March to 2 April at intervals of 3–5 d, and from 16 April to late October at intervals of 10–15 d to cover the seasonal dynamics. All measurements were conducted from 09:30–11:30 hr. In addition, diurnal ecosystem C exchange variations were also measured on 22 March, 2 and 16 April and once a month from May to September. Diurnal variations were measured at 2-h intervals from 09:00–19:00 hr.

For diurnal variation data, exponential regression analyses of ER at each measurement against soil temperature at 0–5 cm (T_s) were performed to calculate the temperature sensitivity of ER at snow melt, spring annual dominance and summer annual and perennial dominance using equation (2):

$$ER = ae^{bT_s}, \quad Q_{10} = e^{10b} \quad (2)$$

where a and b are the fitted parameters and Q_{10} is the temperature sensitivity of ER.

Plant biomass and cover estimations

Vegetation surveys were conducted on 10 May and 20 August 2012. Numbers and heights of all plants in each plot were counted and measured. Above-ground biomass was harvested from a standard sampling quadrant of 1 m × 1 m within each plot and then oven-dried at 70 °C for 48 h in the laboratory. In addition, digital cameras were used to monitor herb growth in the chamber throughout the entire experiment, and plant cover and number calculated for each species. A grid of 2500 squares, each with an area of 1 cm × 1 cm, was overlaid on each image and plant cover determined by counting the number of squares that overlapped a part of the plant. Plant height was measured at each instance of C exchange measurement, and plant biomass was estimated each time when ecosystem gas exchange was monitored, using allometric equations. The allometric equations were estimated by destructive

sampling involving at least 50 individuals for each species in a pre-investigation. The major allometric equations used for biomass estimation are shown in Fig. S1. There was no difference between the biomass values obtained using allometric equations and those obtained by direct measurement.

Temperature, moisture and PAR measurements

Air temperature and precipitation at the experimental site were monitored every 30 min using an automatic meteorological station (Campbell Scientific Corp., Logan, UT, US). Soil moisture (at 0–5 cm) during the snow melt phase was measured by soil coring and converted to soil volumetric water content (SVWC) by multiplying soil bulk density. Soil moisture was measured using time-domain reflectometry (HH2 Moisture Meter; Delta T Devices, Cambridge, UK) in the remaining measurements. Soil temperature at 0–5 cm was measured using a thermocouple probe (JM424 soil temperature measurement system; Tianjin Electronic Co., Tianjin, CN). PAR was measured using a quantum sensor (LI-190SA; Li-Cor, Lincoln, NE, US).

Statistical analysis

To detect differences in response variables among the snow melt, dominance of spring annuals and dominance of summer annuals and perennials phases, mean values of response variables were calculated from each measure-

ment within a phase, then a one-way ANOVA was used to compare differences in NEE, ER, GEE, ET, WUE, soil temperature and SVWC among these dominant phases. Furthermore, plant biomass, biomass of spring annuals and summer annuals and perennials was also compared among the three phases. Correlations between ecosystem C exchange and environmental characteristics and biomass were analysed using bivariate linear regression. Standardized major axis (SMA) regression analysis was performed to analyse differences in slope among the different phases (SMATR, v 2.0 in R software version 3.0.2: <http://www.r-project.org>). Step-wise multiple regression was used to determine relative importance of the various controlling factors for ecosystem C exchange during the growing seasons for the spring annuals and summer annuals and perennials. All data are presented as mean \pm SE unless specified otherwise. All statistical analyses were performed using SPSS 13.0 (SPSS Inc., Chicago, IL, US).

Results

Growth pattern and community dynamics

In the early summer survey, there were 20 herbs, 17 spring annuals and three annuals, while only the three annuals remained in the autumn vegetation survey (Table 1). Spring annuals exhibited faster growth rates than summer annuals in the spring annual dominant phase, but summer annuals had a longer lifespan than the spring annuals and the major period of biomass accumulation of summer

Table 1. The family and name of plant species, photosynthetic pathway (PP), life form (LF), life history traits (LH) and the density of plants (individual m^{-2}) in spring and autumn. SA, spring annual; LA, long lived annual.

Family	Species	PP	LH	Density	
				Spring	Autumn
Boraginaceae	<i>Nonea caspica</i>	C ₃	SA	0.6 \pm 0.4	–
Cruciferae	<i>Alyssum dasycarpum</i>	C ₃	SA	11 \pm 7.7	–
Cruciferae	<i>Alyssum linifolium</i>	C ₃	SA	69 \pm 15	–
Cruciferae	<i>Descurainia sophia</i>	C ₃	SA	0.8 \pm 0.5	–
Cruciferae	<i>Leptaleum filifolium</i>	C ₃	SA	1 \pm 0.4	–
Cruciferae	<i>Tetrademe quadricornis</i>	C ₃	SA	10.7 \pm 5.8	–
Cruciferae	<i>Malcolmia africana</i>	C ₃	SA	2.5 \pm 1.2	–
Chenopodiaceae	<i>Ceratocarpus arenarius</i>	C ₃	LA	68.1 \pm 25.7	23.8 \pm 6.9
Chenopodiaceae	<i>Haloxylon ammodendron</i>	C ₄	LA	3.8 \pm 0.9	–
Chenopodiaceae	<i>Salsola foliosa</i>	C ₃	LA	15.5 \pm 2.8	–
Chenopodiaceae	<i>Salsola passerina</i>	C ₄	LA	2.2 \pm 0.6	11 \pm 2.8
Chenopodiaceae	<i>Salsola subcrassa</i>	C ₃	LA	1.2 \pm 0.6	7.6 \pm 1.8
Compositae	<i>Hyalea pulchella</i>	C ₃	LA	6 \pm 2.9	–
Compositae	<i>Seriphidium santolinum</i>	C ₃	LA	23 \pm 14	–
Crassulaceae	<i>Orostachys cartilagineus</i>	C ₄	LA	0.4 \pm 0.3	–
Geraniaceae	<i>Erodium oxycorymbum</i>	C ₃	SA	61 \pm 8.7	–
Gramineae	<i>Schismus arabicus</i>	C ₃	SA	33.1 \pm 13.3	–
Liliaceae	<i>Gagea subalpina</i>	C ₃	SA	5.1 \pm 1.5	–
Plumbaginaceae	<i>Limonium leptolobum</i>	C ₃	LA	2 \pm 0.7	–

annuals occurred after the death of spring annuals. As such, above-ground biomass of the community showed two peaks in the growing season (Figs 1 and 2): spring annuals accounted for 74.84% of total community biomass, and were the major contributor to the first peak of biomass accumulation, while summer annuals accounted for almost the whole community biomass in August, and contributed to the second peak of biomass accumulation (Fig. 2). Throughout the whole growing season, the dominant plant functional group shifted from the spring annuals to summer annuals and perennials.

Seasonal and diurnal variations in ecosystem C exchange and WUE

Soil temperature exhibited strong seasonal dynamics, with a peak in late June. Soil moisture peaked during the snow-melt phase and in October, but was lower during the herb growing season (May–August; Fig. 3a). Average soil temperature and moisture differed significantly among the three phases (Fig. 3a; $P < 0.05$).

Seasonal patterns of NEE and GEE followed fluctuations in biomass, with peak values in late May. Average C exchange differed significantly among the three phases (Table 2; $P < 0.05$). The highest average NEE, GEE and ER was -0.16 , 0.92 and $1.08 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$, respectively. The highest ET was $1.19 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the highest WUE was $0.99 \mu\text{mol CO}_2 \text{ mmol} \cdot \text{H}_2\text{O}^{-1}$. All these peaks occurred during the spring annual dominant phase. The ecosystem took up C from 16 April to 29 May (Fig. 4a). ER varied during the snow melt phase (Fig. 4a). The diurnal patterns of NEE, GEE and ER were consistent with the diurnal dynamics of PAR and soil temperature (Fig. 4); however, all three decreased dramatically after

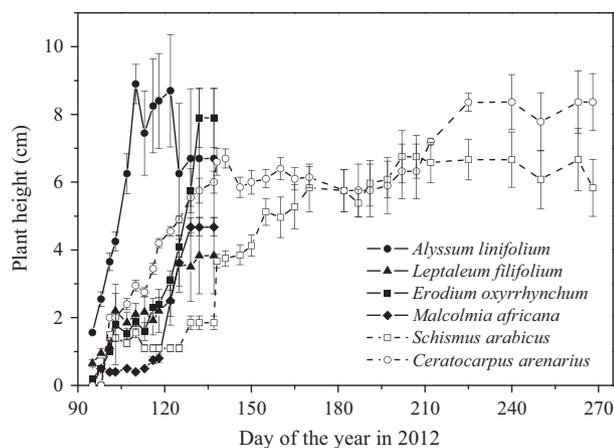


Fig. 1. Dynamics of plant height of dominant spring annuals (*Alyssum linifolium*, *Leptaleum filifolium*, *Erodium oxycarrhynchum*, *Malcolmia africana*) and summer annuals (*Schismus arabicus*, *Ceratocarpus arenarius*).

June and showed small diurnal variations (Fig. 4b,c), even though temperature and PAR remained comparable to values in the spring annual dominant phase (Fig. 4d–f).

Biotic and abiotic controlling factors of NEE

Net ecosystem C exchange was positively correlated with soil moisture ($r^2 = 0.41$) and plant biomass ($r^2 = 0.50$) during the spring annual dominant phase, but negatively correlated with soil temperature (snow melt: $r^2 = 0.52$, spring annual: $r^2 = 0.41$, summer annuals and perennials: $r^2 = 0.32$) at all three phases (Fig. 5a–c). During the spring annual dominant phase, GEE was positively correlated with plant biomass and soil moisture, but negatively correlated with soil temperature (Fig. 5d–f). GEE was positively correlated only with plant biomass during the summer annual and perennial dominant phase (Fig. 5f). ER was positively correlated with soil temperature and negatively with soil moisture during the snow-melt phase (Fig. 5g,h). ER showed the same relationship with plant biomass and soil moisture as GEE in the spring annual dominant phase, and the slope of ER–biomass was much lower than that of GEE–biomass (Fig. 5d–i). At a diurnal scale, both NEE and GEE were correlated positively with daily variations in PAR and soil temperature during the spring annual dominant phase, but there was no relationship of NEE with PAR and soil temperature during the summer annual and perennial dominant phase (Fig. 6). ER was correlated exponentially with daily soil temperature, and Q_{10} values followed the order of snow-melt phase (2.6) > spring annual dominant phase (1.7) > summer annual and perennial dominant phase (0.56; Fig. 7).

Step-wise regression demonstrated that soil temperature alone explained 70.8% of the temporal ER variation

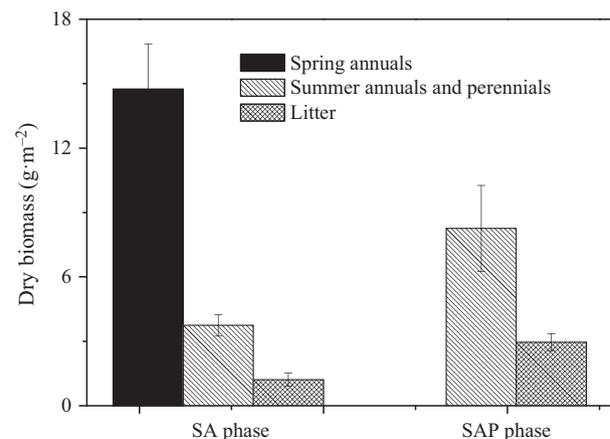


Fig. 2. Dry biomass of soil surface (ephemerals, annuals and litter) in spring annuals dominant phase (SA) (sampled in mid-May) and summer annuals and perennials dominant phase (SAP) (sampled in mid-August).

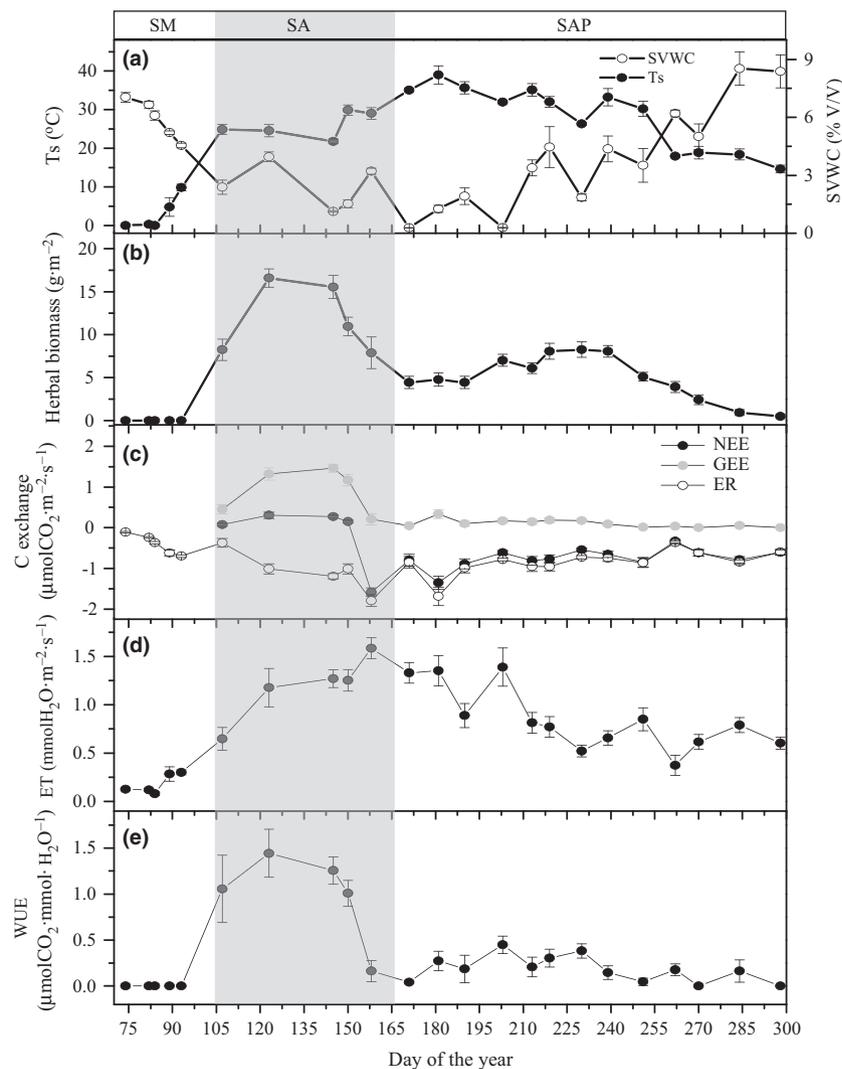


Fig. 3. Seasonal dynamics of soil temperature (T_s , **a**), and soil volumetric water content (SVWC, **a**), herbal biomass (**b**), net ecosystem carbon exchanges (NEE, **c**), gross ecosystem carbon exchange (GEE, **c**), ecosystem respiration (ER, **c**), ecosystem evapotranspiration (ET, **d**), ecosystem water-use efficiency (WUE, **e**) at three phases of snow-melting (SM), spring annuals dominant phase (SA) and summer annuals and perennials dominant phase (SAP).

Table 2. The averaged net carbon exchange (NEE), gross carbon exchange (GEE), and ecosystem respiration (ER), ecosystem evapotranspiration (ET), and ecosystem water-use efficiency (WUE) at snow-melting (SM), ephemeral dominant phase (EP) and long-lived annual dominant phase (AN).

	NEE ($\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$)	GEE ($\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$)	ER ($\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$)	ET ($\text{mmol m}^{-2}\cdot\text{s}^{-1}$)	WUE ($\mu\text{mol CO}_2 \text{mmol H}_2\text{O}^{-1}$)
SM	-0.30 ± 0.02 a	0 a	0.30 ± 0.02 a	0.18 ± 0.02 a	0 ± 0 a
EP	-0.16 ± 0.03 b	0.92 ± 0.08 b	1.08 ± 0.08 b	1.19 ± 0.04 b	0.99 ± 0.06 b
AN	-0.74 ± 0.03 c	0.10 ± 0.02 a	0.84 ± 0.03 c	0.84 ± 0.07 c	0.18 ± 0.03 a

Different small letters indicate significant difference among investigation phases at $P < 0.05$ level.

observed during the snow melt phase (Table 3). In contrast, herb biomass alone accounted for 56.3%, 82.0%, and 26.1% of the temporal NEE, GEE and ER variation, respectively, during the spring annual dominant phase (Table 3). During the summer annual and perennial

dominant phase, the herb biomass and soil temperature together accounted for 32.3% of the temporal NEE variation, while herb biomass alone accounted for 48.0% of temporal GEE variation, and soil temperature alone accounted for 31.1% of temporal ER variation (Table 3).

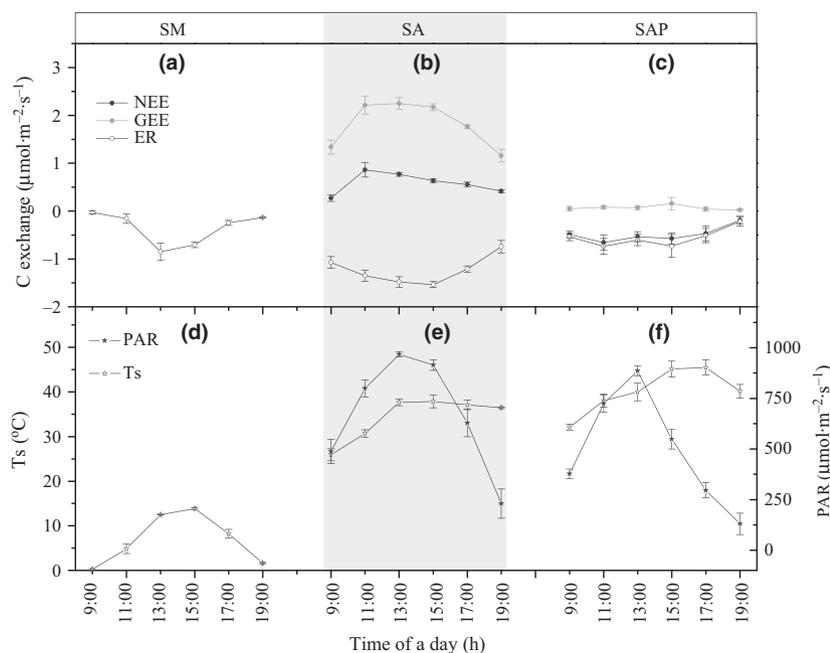


Fig. 4. The typical diurnal changes of net ecosystem carbon exchanges (NEE), gross ecosystem carbon exchange (GEE), ecosystem respiration (ER), soil temperature (T_s) and photosynthetically active radiation (PAR) at three phases of snow-melting (a and d, Mar 22), spring annuals dominant phase (b and e, May 24) and summer annuals and perennials dominant phase (c and f, July 21).

Discussion

In this study, we found that ecosystem C uptake in the Gurbantungute Desert was confined to a very short period (mid-April to late May) and was mainly dependent on growth of spring annuals. The factors controlling NEE varied temporally and resulted from interactions between plant functional group and environmental factors. During the snow-melt phase, the ecosystem showed a net C release, and NEE was largely determined by soil temperature. However, in response to increased growth of spring annuals after snow melt, the ecosystem became a C sink as herbaceous community biomass increased under favourable soil moisture and temperature conditions. After the spring annuals died, summer annuals and perennials contributed only slightly to GEE. As a result, GEE did not cancel out ER, and this led to a net ecosystem C release.

Effects of temperature on ecosystem C exchange

The results supported our prediction that the effects of temperature on NEE depend on covariation of plant functional traits and soil moisture within the community. During the snow-melt phase, ER exhibited a high soil temperature sensitivity, with a Q_{10} of 2.6, which contributed to the C release. During the spring annual dominant phase, higher temperatures were usually accompanied by lower soil moistures, which depressed their growth. As a

result, soil temperature was negatively correlated with GEE (Fig. 5d). When the summer annuals and perennials dominated the community, both GEE and ER were positively correlated with temperature, due to the larger stimulation of temperature on ER than on GEE, as suggested by the higher slope of $ER-T_s$ than $GEE-T_s$, temperature exerted negative effects on NEE, in line with previous studies in a typical temperate steppe (Xia et al. 2009). Thus, temperature had adverse effects on seasonal NEE by inhibiting the growth of spring annuals in their dominant phase and stimulating ER in the summer annual and perennial dominant phase. This emphasizes the ecological significance of seasonal synchronization of precipitation and temperature with respect to ecosystem C exchange.

Effects of soil water content on ecosystem C exchange

Consistent with the first prediction, NEE exhibited seasonal variations, with C uptake in the spring annual dominant phase and C release at snow melt and in summer annual and perennial dominant phases. Moreover, controlling factors for NEE varied with the transition in plant phenology, and the effects of precipitation on NEE also varied throughout the growing season. Despite the high soil moisture levels, soil temperature was responsible for temporal variations of ER during the snow melt phase (Table 2). In the spring annual growing season, particularly during the fast growth period (April–May), the higher

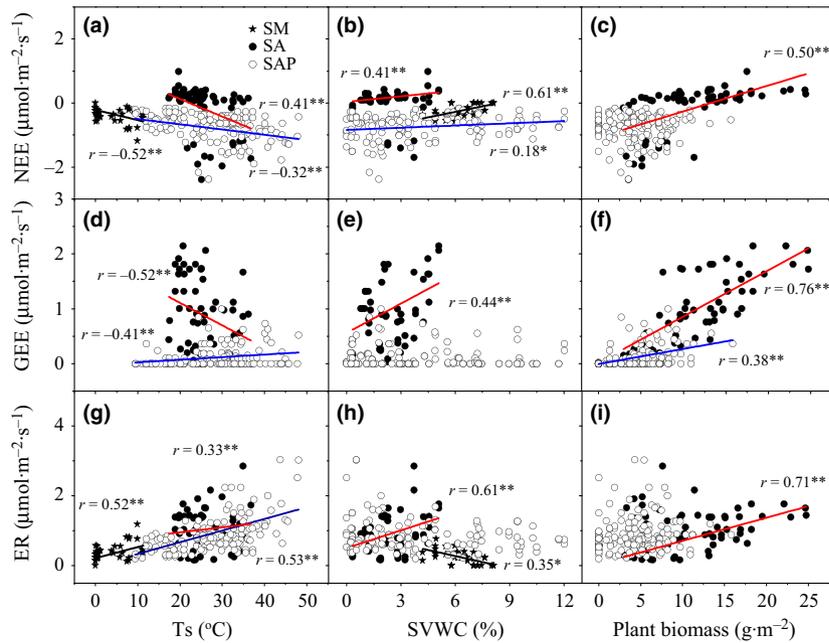


Fig. 5. Seasonal dependence of net ecosystem carbon exchange (NEE, **a-c**), gross ecosystem carbon exchange (GEE, **d-f**) and ecosystem respiration (ER, **g-i**) on soil temperature (T_s), soil volumetric water content (SVWC), plant biomass at snow-melting phase (SM), spring annuals dominant phase (SA) and summer annuals and perennials dominant phase (SAP).

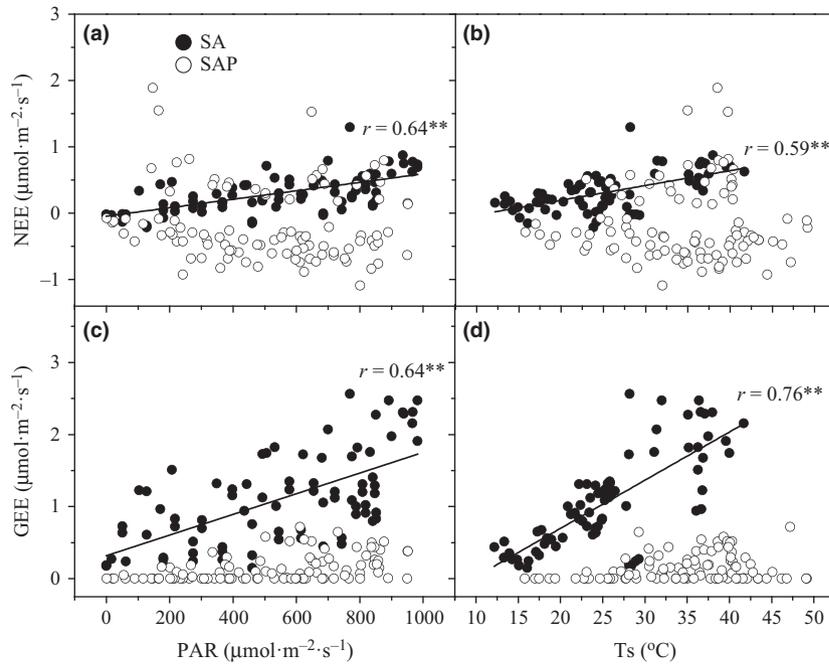


Fig. 6. Diurnal dependence of net ecosystem carbon exchanges (NEE, **a & b**) and gross ecosystem carbon exchange (GEE, **c & d**) on PAR and soil temperature (T_s) at spring annuals dominant phase (SA) and summer annuals and perennials dominant phase (SAP).

GEE–SVWC slope relative to the ER–SVWC slope indicates that the positive effects of soil moisture on GEE were stronger than on ER ($P < 0.01$). As a result, the ecosystem exhibited a net C uptake; however, after the spring annu-

als died, NEE depended primarily on ER and was insensitive to SVWC. The different response magnitudes of NEE to soil moisture, as indicated by the slope of NEE–SVWC, between spring annual dominant phase and summer

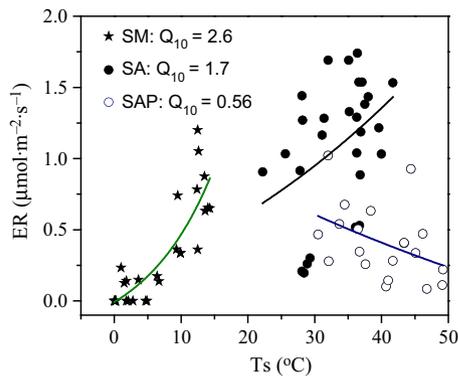


Fig. 7. The dependences of ecosystem respiration (ER) on soil temperature in snow-melting phase (SM), spring annuals dominant phase (SA) and summer annuals and perennials dominant phase (SAP). Q_{10} was the temperature sensitivity of ER.

Table 3. The results of multiple linear regression of net carbon exchange (NEE), gross carbon exchange (GEE), and ecosystem respiration (ER) on soil temperature (T_s), soil volumetric water content (SVWC), herbal biomass (HB) at snow-melting (SM), ephemeral dominant phase (EP) and long-lived dominant phase (AN).

Phase	Regression Model	R^2	P value
SM			
ER	$ER = 0.207 + 0.062 \cdot T_s$	0.71	<0.001
EP			
NEE	$NEE = -1.26 + 0.055 \cdot HB$	0.56	<0.001
GEE	$GEE = -0.243 + 0.088 \cdot HB$	0.82	<0.001
ER	$ER = -1.017 + 0.033 \cdot HB$	0.26	<0.001
AN			
NEE	$NEE = -0.231 + 0.044 \cdot HB - 0.025 \cdot T_s$	0.32	<0.001
GEE	$GEE = -0.034 + 0.043 \cdot HB$	0.48	<0.001
ER	$ER = -0.237 + 0.02 \cdot T_s$	0.31	<0.001

annual and perennial dominant phase ($P < 0.01$) were closely related to characteristics of these two functional groups and their WUE. Previous studies showed higher photosynthesis in spring annuals, reaching $15.1 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ in *Erodium oxyrrhynchum*, $18.2 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ in *Alyssum linifolium*, $23.6 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ in *Malcolmia africana* and $33.1 \mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$ in *Malcolmia scorpioides* (Qin et al. 2007). The high photosynthesis and growth rates of spring annuals resulted in a high ecosystem WUE ($0.99 \mu\text{mol CO}_2 \text{ mmol}^{-1} \cdot \text{H}_2\text{O}$) compared to that in the summer annual and perennial dominant phase ($0.18 \mu\text{mol CO}_2 \text{ mmol}^{-1} \cdot \text{H}_2\text{O}$). This demonstrates that WUE plays an important role in the direction and magnitude of responses of NEE to soil water availability. This is similar to the ecosystem response to invasion of exotic forbs (*Erodium cicutarium*) in the North America prairie reported previously (Brooks 1999). *E. cicutarium* has a similar functional

role to *E. oxyrrhynchum* in the present study, and *E. oxyrrhynchum* exerted significant effects on NEE. This finding was partly confirmed in eddy covariance measurements, which demonstrated a higher NEE in a wet year because of increased WUE (Liu et al. 2012). Thus, inclusion of WUE in climate change models can improve prediction accuracy with respect to increasing precipitation variation in desert ecosystems.

The importance of spring annuals in ecosystem C exchange

Due to discrepancies in plant growth rate and lifespan between spring annuals and summer annuals and perennials, spring annuals accounted for 74.84% of the plant biomass in spring and early summer, and GEE derived from the spring annual dominant phase accounted for more than 80% of total GEE throughout the growing season (mid-March–late October). This is consistent with our third prediction that spring annuals take up more CO_2 through photosynthesis. Moreover, GEE was correlated positively with NEE, and WUE was highest during the spring annual dominant phase, suggesting that spring annuals are well acclimated to this temperate desert and are highly efficient in utilizing water and sunlight. The Intergovernmental Panel on Climate Change has predicted an increase in annual precipitation and larger inter- and intra-annual variations of precipitation in this region of China in the future (IPCC 2007). Increasing precipitation during the spring annual growing season will increase the growth and biomass accumulation of spring annuals, leading to positive impacts on NEE and ecosystem C interception. In contrast, increased precipitation after the death of spring annuals will promote ER. The limited stimulation of precipitation on GEE in the summer annual and perennial dominant phase is because of the low WUE of the annuals, which in turn may adversely affect NEE and increase ecosystem C release. Thus, the interaction of precipitation timing with plant growth determines ecosystem C exchange in this desert.

Furthermore, the biomass of summer annuals and perennials contributes little to community biomass, and therefore has a limited effect on GEE. However, given the temporal continuity of the three phases, summer annuals and perennials account for most of the cover and biomass of the community after the death of spring annuals, and are thus indispensable constituents of this temperate desert. In particular, increased cover of summer annuals and perennials could lead to a reduction of ER by decreasing soil temperature. Therefore, we infer that if increased precipitation occurs after death of spring annuals, the effects on NEE would rely on the relative impacts of soil moisture and temperature.

Study limitations

The multi-year average precipitation at the study site was 163 mm. The present study was conducted in a dry year (102 mm precipitation), and the key factors that control NEE depend closely on interactions among precipitation, plant growth and temperature. Given the large variations in the amount and timing of precipitation, we infer that inter-annual shifts in precipitation can significantly alter plant growth and productivity, giving rise to alterations in the factors controlling NEE. Our results also demonstrate that alterations in community structure can shift factors that control seasonal NEE variations, in contrast to processes in evergreen forests and grasslands, which exhibit only slight variation in plant functional types. The high level of temporal NEE variation observed in our study suggests that we should examine alterations in factors that control seasonal NEE variations to accurately predict and evaluate the carbon budget in the temperate desert steppe.

Acknowledgement

This study was supported by the National Natural Science Foundation of China (No. 41371079 & 31370010), the Strategic Priority Research Program of China (No. XDA05050305) and the National Natural Science Foundation of China (No.41371004).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. The major allometric equations used for biomass estimation.